Proceedings of the American Academy of Arts and Sciences.

Vol. XLI. No. 13. — September, 1905.

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IV. — *ON THE KARYOSPHERE AND NUCLEOLUS IN THE SPERMATOCYTES OF SCOLOPENDRA SUBSPINIPES.*

By Maulsby W. Blackman.

With a Plate.

THE SPERMATOGENESIS OF THE MYRIAPODS.

IV.—ON THE KARYOSPHERE AND NUCLEOLUS IN THE SPERMATOCYTES OF SCOLOPENDRA SUBSPINIPES.*

By Maulsby W. Blackman.

Presented by E. L. Mark. Received June 14, 1905.

In making a comparative study of the spermatogenesis of different species of chilopods the phenomena observed in Scolopendra subspinipes are in some respects so markedly different from those already reported as characteristic of S. heros (Blackman, :02 and :05) as to warrant their treatment in a separate paper. The most striking differences are dependent upon the fact that a large plasmosome, or true nucleolus, is present within the nucleus of the spermatocytes of S. subspinipes during stages of mitotic inactivity, while in the cells of S. heros no such structure is to be found. The presence of this body in S. subspinipes seems to necessitate a corresponding variation in the behavior of the chromatin. Although these differences are often quite marked, the process is essentially similar in the two species.

The material upon which this paper is based was collected by the author near Flatts, Bermuda, during July, 1903. I am glad of this opportunity of thanking Dr. E. L. Mark, director of the Bermuda Biological Station, for numerous courtesies extended to me while working in the laboratory.

The testes obtained from Scolopendra subspinipes are not so far advanced in development as those of S. heros, used in observations recorded in my former papers (Blackman, :03 and :05). Very few spermatozoa, spermatids, and secondary spermatocytes are to be found, nearly the entire bulk of the testis consisting of growing spermatocytes and cells in what I have elsewhere (:05) designated as the vesicle stage. The proportion of cells of the smaller type does not seem to be as great as that found in S. heros (Blackman, :01, :05) or in S. morsitans (P. Bouin, :03). This may be, and probably is, due to the age of

* Contributions from the Bermuda Biological Station for Research, No. 8.

the individuals; for I have concluded from a study of the cells of the two types in S. heros that the difference in size is due to differences in nutrition.

The testes were fixed in Gilson's fluid, embedded in paraffine, and reduced to sections 3 to 5 micra thick. These were stained in Heidenhain's iron-haematoxylin (some were counterstained with Congo red), and studied under a magnification of from 1200 to 1800 diameters.

The spermatogonia of S. subspinipes in the resting stage are similar in all respects to those of S. heros. They are small cells containing an oval nucleus, in which no indication of chromatin can be observed except the large, deeply staining nucleolus-like body, the karyosphere. During the prophase small granular aggregations of chromatin appear (Figure 1), and at the same time the karyosphere becomes so altered as to show conclusively that, as in the sister species, the chromosomes are derived from its substance.

After the formation of the chromosomes from the karyosphere in S. heros nothing of this body remains except the accessory chromosome. In the present species, however, the residue is different. It consists of two parts, a small, deeply staining chromatic body, the accessory chromosome, and a larger, less dense part, the plasmosome (Figure 1). The latter part does not retain the haemotoxylin, but is nearly colorless, or assumes a reddish-brown tint, when the haematoxylin is followed by Congo red. During the later part of the prophase the plasmosome is dissolved, and in the metaphase and later stages of mitosis no indications of such material are to be found (Figure 2).

The phenomena occurring during the later stages of the last spermatogonium seem to be identical in all essential respects to those already described as existing in S. heros. At the end of the anaphase the chromosomes are massed together so closely at opposite poles of the elongated cell as to make their outlines indistinguishable (Figure 2). Later, during the telophase, these chromosomes still aggregated into a dense mass, lengthen out into slender granular segments (Figure 3). A single element, however, the accessory chromosome, does not assume this granular condition, but retains its homogeneous appearance and is on this account very conspicuous (Figure 3).

Upon the reconstruction of the nuclear membrane the segments of chromatin become distributed throughout the nuclear space (Figures 4, 5), causing the cells at this stage to bear a close resemblance to the sperm cells of insects in the spireme condition. Here, however, the chromatin is not a continuous thread, as it is said to be in the cells of many animals,

but is in the form of a number of granular segments, one half as numerous as the ordinary chromosomes of the spermatogonia.

These chromosomes are produced by the union in pairs of the chromosomes of the division period. That this is an end to end union is very strongly indicated, although not definitely proved, by the appearance of the chromatin segments at this stage. In Figures 4 and 5 the nuclear vesicle is occupied by a number of slender granular chromatin segments, each of which is bent near its middle, forming a V-shaped figure. At the angle of the V, which doubtless represents the point of union of the two component elements, the chromatin is often interrupted in such a manner that the halves of the segment seem to be connected by only a strand of linin. These conditions in Scolopendra are quite similar to those described by Montgomery (:00) in Peripatus, and later (:01) in Hemiptera, and they lead to the same conclusion as did the more convincing observations made by Sutton (:02) on Brachystola. The latter author has shown conclusively that the synapsis of the chromosomes occurs during the telophase of the last spermatogonium, and that it is brought about by an end to end union of entire spermatogonial chromosomes.

Thus in S. subspinipes the pseudo-reduction of the chromosomes is accomplished in exactly the same manner as in S. heros. Up to this stage (Figure 4) the appearance of the accessory chromosome has been entirely similar to that in S. heros, but from now on the behavior of all of the chromatin is quite noticeably different. This is evidently due to the introduction within the nucleus of a new structural element, — the true nucleolus, or plasmosome.

The first indication of the nucleolus in the spermatocyte is seen at the stage when the nuclear membrane has just been re-formed (Figure 5). At this time a transparent, non-stainable structure appears upon one side of the accessory chromosome. This fundament of the nucleolus at first has very much the appearance of a vacuole occupying one side of the accessory chromosome (Figure 5).

In the telophase of the last spermatogonial division the accessory chromosome, when it first becomes distinguishable from the other chromosomes, is of an oval shape (Figures 3, 4), but after the origin of the plasmosome the compound element thus arising is at first spherical. The chromatin representing the accessory chromosome assumes a crescent shape and nearly surrounds the unstained part — the plamosome. In this manner the accessory chromosome forms one half or more of the outline of the sphere (Figures 5, 8 *b*).

With the reappearance of the nuclear membrane the cell enters upon a period of phenomenal growth and the nucleolus increases in size very rapidly, while the accessory chromosome remains of nearly the same size. Stages in this growth of the nucleolus are shown in Figures 6, 7, and 8, *b, c, d, e.* As the nucleolus grows it also changes in its reaction to stains, and assumes the diffuse brownish tint characteristic of the plamosome when stained with iron-hamotoxylin (Figure 8 *c*). Its shape also is so altered that from now on it is an approximate sphere, upon one side of which lies the deeply stained accessory chomosome. This body, which has again assumed an oval shape, is usually not embedded in the plasmosome, but is closely apposed to one side of it (Figures 8 *f*, 9). Quite often there is a cup-like depression in the plasmosome at the place where the accessory chromosome comes into contact with it (Figure 10).

It is during the period represented by Figures 4 to 19 that the most striking and interesting differences between the germ cells of Scolopendra subspinipes and S. heros occur. These variations, as I have already intimated, primarily concern the arrangement and behavior of the chromatic structures.

The conditions in S. heros are briefly as follows: Upon the reconstruction of the nuclear membrane after the last spermatogonial division, the cells, now containing the number of chromatin segments characteristic of spermatocytes, "enter upon a period remarkable for the extraordinary changes which take place in their structure." Of these changes the most remarkable are the enormous increase in the size of the cells and the peculiar and characteristic arrangement of the chromatin.

Concerning the growth of the cells in S. heros it is sufficient to say that the diameter of the large spermatocytes is about ten times that of the spermatogonia from which they arise. As regards the chromatin structures, I may quote from one of my papers cited (:03): "As the cell continues in its growth the chromatin segements become larger and more diffuse. They no longer retain the stain with the persistency which has characterized them heretofore. Gradually they break down and their substance is accumulated about the accessory chromosome, thus seemingly increasing this element greatly. This process continues until all of the chromatin of the cell is aggregated in one large, intensely staining body situated peripherally in close contact with the nuclear membrane." This body, the karyosphere, is not a homogeneous mass of chromatin, but, "on the contrary, is a rather complex structure, consisting of chromatin, linin, and karyolymph." The chromatin composing the karyosphere is in the condition of a very fine spireme, which is so

densely massed as to present the appearance under moderate magnification of a homogeneous sphere of chromatin. It is only in thin sections and with high magnification (1200 to 1800 diameters) that the spireme character is shown. Later, during the prophase, the chromosomes arise from this mass by a mere unwinding of the chromatin threads. When this process is completed nothing remains of the karyosphere but the accessory chromosome. There is apparently no nucleolar material contained in it, as no residue can be found within the nucleus and no such structure can be seen at any previous stage.

I shall now describe the changes during the same period in S. subspinipes and compare the processes in the two species. During the telophase of the last spermatogonium the appearance of the cells of the two species is identical, but at the time of the formation of the nuclear membrane the true nucleolus arises in S. subspinipes in close contact with the accessory chromosome and grows rapidly as the cell increases in size. Thus the conditions in the two species are slightly different, and it is to be expected that the subsequent behavior of the cells would also vary.

In S. heros it was impossible to follow in detail the process of the massing of the chromatin into the karyosphere. In S. subspinipes, however, this process, for reasons which I shall soon make plain, can be followed much more satisfactorily. In this species the chromatin, instead of becoming closely aggregated about the accessory chromosome, is deposited in a rather thin layer upon the periphery of the large nucleolus, or plasmosome. This structure, staining so differently from the chromatin, furnishes an excellent background, by means of which the various stages in the formation of the karyosphere may be studied with ease.

In S. subspinipes, as in S. heros, the formation of the nuclear membrane around the chromosomes may be taken as marking the transition from spermatogonium to spermatocyte. In one species, precisely as in the other, this stage ushers in a period remarkable for the concentration of the chromatin. As the cells grow the chromosomes gradually become much more diffuse and therefore stain less deeply. During this time the nucleolus, still in close apposition to the accessory chromosome (Figure 8 *b*), increases in size so rapidly that its volume is soon several times that of the accessory chromosome (Figure 8 *c*, *d*).

Shortly after the stage shown in Figure 8 *d*, the nucleolus seems also to change somewhat in its staining reaction. Irregular areas upon its periphery now show a marked affinity for chromatin stains (Figures 6, 7, 8 *e*), causing it under moderate magnification to appear of a uniform gray color.

With higher amplification, however, it is readily seen that this change is due to the deposition of some of the chromatic threads upon the surface of the nucleolus. These deposits are in the form of very diffuse spiremes, which are similar to the segments which are still free in the nuclear space (Figure 6). The nucleolus as seen in profile no longer presents an even contour, but at the places where the dark areas are found the diameter of the mass is increased (Figure 8 *e*). It is thus evident that loose threads of chromatin are being merely applied to the outside of the nucleolus, not embedded in its substance. The accessory chromosome still preserves the same relation to the nucleolus as before, being closely apposed to one side of this structure (Figure 8 *d*, *e*).

As the cell continues to grow the free chromatin within the nucleus becomes more and more scanty (Figures 6, 7), until soon only a few chromatin segments are to be seen where formerly there were many (Figure 7). Finally, in the "vesicle" stage (Figures 9–13), no chromatin is to be found in the nucleus except that which is massed about the nucleolus to form the karyosphere.

During the growth period of the spermatacyte the nucleolus has increased very markedly in size (Figure 8 *e*, *f*). This is due both to the increase of nucleolar material and to the deposition of chromatin upon the periphery of the nucleolus. At the time of the vesicle stage the appearance of the karyosphere* varies considerably in different cells, this variation being due to the different manner in which the chromatin is arranged with regard to the nucleolus. Different appearances presented by the karyosphere at this stage are shown in Figures 8 *f*, and 9–13. Usually the chromatin is distributed more or less unevenly over the surface of the nucleolus (Figures 8 *f*, 9) but often it forms a nearly complete (Figures 11, 13) or complete (Figures 10, 12) layer about it, thus causing the karyosphere to stain very intensely. In preparations stained with haemotoxylin and Congo red the karyosphere appears black when the surface is in focus, but when the centre is in focus the middle portion of the body shows a reddish-brown coloration, thus disclosing the presence of nucleolar material. Likewise, when a portion of one side of the karyosphere has been removed in the process of sectioning, the true structure of the body is shown. Figure 10, representing such a condi-

* In my former papers I have described the karyosphere as a highly organized structure found within the nucleus and containing "chromatin (in a granular, reticular, or spireme form), karyoplasm,—i. e., linin,—and karyolymph. It is in fact a miniature nucleus." It is now seen that it may be still more complex, since it may also contain nucleolar material.

tion, shows the outer layer of intensely staining chromatin and the inner nucleolar material, containing several vacuoles.

More commonly, however, the karyosphere exhibits the reticular appearance represented in Figures 8*f*, 9. Here the chromatin is very plainly of the nature of a superficial spireme or a reticulum, which does not completely invest the nucleolus. The appearance of the karyospheres of this nature is strikingly similar to that of a small nucleus in which the chromatin is spread out over the periphery of the nuclear area in flaky masses (Figure 9).

Meanwhile the accessory chromosome has undergone no apparent change, and throughout the growth period has preserved the same relation to the nucleolus which it had during the early spermatocyte stages (Figures 5–11). Occasionally an accessory chromosome is not to be seen, owing to the fact, doubtless, that the section is cut in such a plane that the chromosome is concealed behind the karyosphere or does not lie in the same section with it (Figures 11, 12).

In S. subspinipes, just as in S. heros, a number of small granular masses of a deeply staining substance are scattered throughout the nucleus. These stain similarly to chromatin; inasmuch, however, as such masses are also present at various places in the cytoplasm outside the nucleus, it seems probable that they are not chromatin, but metaplasm — i. e., that they are either food material or by-products of the cell's activity.

In S. heros the first changes in the active prophase of the division of the first spermatocyte manifest themselves in the cytoplasmic structures; they consist in the dissolution of the archoplasm and the migration of the centrosomes. In S. subspinipes this is not true. Here the first marked change affects the chromatin. The chromosomes do not arise as distinct entities from the karyosphere by a simple disentanglement of the spireme, but the chromatic portion of the karyosphere is merely detached in the form of a varying number of flaky reticular masses, which thus come to lie free in the nuclear vesicle. These spongy masses of chromatin do not represent single chromosomes, for they later break up into several smaller masses, which soon take on the form characteristic of tetrads in the prophase. Figure 14 represents a spermatocyte in the very early prophase, in which the chromatin has just left the karyosphere. There are several chromatin masses; of these the larger one contains nearly all of the chromatin. Figures 15–18 represent slightly different stages, a little older than that shown in Figure 14. In Figure 15 the chromatin is in several masses, of which the larger ones doubtlessly represent several chromosomes. In Figures 17 and 18 the chromatin has separated into

distinct chromosomes, and some of these already show plainly their tetrad nature. In Figures 15 and 16 not all of the chromatin has as yet left the nucleolus, several diffuse flaky masses being still spread out over its surface.

After leaving the karyosphere, the chromatin soon breaks up into a number of diffusely granular segments, each representing a chromosome. These segments are not at first very similar to those found in S. heros, as they are not long slender chromatic filaments, but much shorter and thicker. They, however, undergo the same changes (Figure 19); i. e., they are divided first longitudinally and later crosswise. The latter division takes place at the point where in the preceding telophase the spermatogonial elements united. These soon come to resemble exactly the tetrads found in the sister species. Many variations and distortions of the tetrad are to be found, just as in S. heros, but, as in that species, they all may be referred to the typical cruciform or double-V figures described by Paulinier ('99) and McClung (:00).

These quadripartite bodies arise in the following manner. In the early prophase the chromatin of the cell is in the form of a number of granular segments, each one of which represents one of the bivalent chromosomes obtained by the end to end union in pairs of the univalent chromosomes of the spermatogonium. Each of these segments splits longitudinally throughout its entire length, thus forming a double thread of chromatin. Soon after this cleavage is effected, each half of the chromosome divides near the middle of its length,— i. e., at the point at which the component elements united to form the bivalent chromosome,— and the adjacent ends produced by this cross division become drawn out in the same direction and perpendicular to the axis of the original thread, but the adjacent ends resulting from the cross division of one half of the thread move in a direction opposite to that of the other half, thus forming the cross-shaped figures so common in the spermatocyte prophase (Figure 19).

In later stages the chromosomes come together more closely, thus causing the chromosome to become more compact and to lose its granular appearance. By this condensation the planes of cleavage separating the four component chromatids, which are quite pronounced in earlier stages (Figure 19), become so masked that they can no longer be distinguished. The chromosomes of this stage — the late prophase — have typically the four-lobed appearance represented in Figure 20; but some of them may be so distorted as to show little evidence of relationship with the tetrads of an earlier stage.

During the early prophase, up to a time when the tetrads have begun to be formed, the accessory chromosome remains apparently unchanged. It is still a small, deeply staining, homogeneous body closely apposed to one side of the plasmosome. Later, when the other chromosomes have already assumed the tetrad shape and have begun the process of condensation, it leaves this position, and thereafter may lie in any part of the nucleus. Owing to the ordinary chromosomes being of irregular form during the late prophase (Figure 20), and to their being approximately equal in size to the accessory chromosome, the latter is in many cells not distinguishable from them. Consequently it has been impossible to trace the later history of the accessory chromosome in S. subspinipes with as much certainty and in such detail as has been done in S. heros (Blackman, :05). However, I can say that the accessory chromosome, unlike the other chromatic elements, undergoes but one — a longitudinal — division.

Thus it is certain that the behavior of the modified chromosome in the two species of Scolopendra which I have studied is similar, at least in all essential particulars. In both species the accessory chromosome is produced not by the union of two spermatogonial chromosomes during synapsis, as the other chromosomes are, but is derived from one of the spermatogonial elements directly, being in no way altered by synapsis. Since the object of the reduction division is the separation of the chromosomal elements which conjugated during the telophase of the last spermatogonium, it naturally follows that the accessory chromosome, not having taken any part in this conjugation, does not undergo a reduction division. In Scolopendra heros (Blackman, :03, :05), as well as in many insects, Pyrrhocoris (Henking, '91), Anasa (Paulmier, '99), Orthoptera (McClung, :02, Sinéty, :01, Sutton, :03), the absence of this element in one half of the spermatids has been demonstrated. This is also true for S. subspinipes.

At the end of the growth period, during the vesicle stage, the inner, lightly staining portion of the karyosphere, i. e., the nucleolus, often contains several small clear spaces. As these show no reaction whatever to the stains, and as they are bounded by a definite spherical outline, it is probable that they are vacuoles filled with a fluid or gaseous substance. Before the beginning of the prophase the conditions are such that these structures are not often visible. It is only in such cases as that represented in Figure 10, where a part of the karyosphere has been removed in sectioning, that they may be observed. Later, however, in the prophase, when the chromatic portion of the karyosphere has become de-

tached, leaving the nucleolus plainly visible, the conditions for observing them are favorable. At this time there are usually three or four of these vacuoles, their diameters being about one sixth to one tenth that of the plasmosome (Figures 14–18). They are clear, transparent, unstained spherules bounded by a definite outline, but enclosed in no distinguishable membrane. Later, as the prophase advances and the tetrads take on their characteristic form (Figures 19, 20), these vacuoles increase both in size and number, until, just before the nuclear membrane breaks down, they are often so numerous that the nucleolus is a spongy mass bearing little resemblance to its previous appearance. During this time the plasmosome has not appreciably altered in size; however, in the very late prophase, only a little of the original material remains.

This, I believe, might be explained on the supposition that the vacuoles represent material — probably hyaloplasm — obtained from without, while the nucleolus at the same time gives off material to the nucleus. The material thus gained by the nucleus may represent merely a by-product of cell metabolism, but the fact that the nucleolus degenerates immediately preceding cell division might be taken to indicate a more important function. Three explanations concerning the purpose and fate of the nucleolus suggest themselves: (1) the material may be used for the nutrition of the cell in general, (2) it may be used directly in the formation of the spindle fibres, or (3) it may contribute to the achromatic portion of the chromosomes. I believe that the first of these alternatives is realized in the case of S. subspinipes. In S. heros, where the archoplasmic structures are very well developed, no nucleolus is to be found at any stage of the spermatocyte. It further seems very often to be true that where the proportion of chromatin in the cell is especially large, as in the spermatocytes of insects and amphibians, no nucleolus whatever is present, thus pointing to the independence of the chromosomes. On the other hand, in cells in which there is a great preponderance of cytoplasm, as in egg cells, nucleolar structures are of very general occurrence.

The behavior of the chromosomes during the two following mitoses is so similar to that already described in S. heros that it hardly requires separate description. The result of the two spermatocyte divisions is four spermatids from each primary spermatocyte. Of these four, two contain one more chromosome each than do the other two, just as is the case in S. heros. The accessory chromosome is not divided in the first mutosis, but goes entire to one cell. In the second division, when the other chromosomes are undergoing a reduction division, this divides longi-

tudinally. In the spermatid it is for a time distinguishable from the other chromosomes on account of its homogeneous condition.

No traces of a nucleolus are to be seen at any stage after the late prophase or early metaphase of the first spermatocyte. No such structure reappears during the short prophase of the second spermatocyte, nor have I observed it in the few spermatids to be found in my material. It would seem that, in S. subspinipes at least, the nucleolus is present only in stages of protracted mitotic inactivity.

The principal facts of interest presented in this paper are due to the presence of a true nucleolus or plasmosome in the nucleus of the sperm cells during the so-called resting stages of mitosis. The presence of this body seems to result in a considerable difference in the behavior of the chromatin and in the structure of the karyosphere. Carnoy ('85) in his "Cytodiérèse chez les arthropodes" has divided nucleolar bodies into four classes, his conclusions being based in part upon observations on the spermatogenesis of various Chilopods. These classes are as follows: "(*a*) les nucléoles nucléiniens; sperules de nucléine amorphe, ou remassée en peleton serré; (*b*) les nucléoles plasmatiques, masses albuminoides renfermant de la plastine; (*c*) les nucléoles mixtes, qui sont constitués par la réunion des deux espèces précédentes en un corps unique, où chacune se maintient cependant sous une forme figurée; (*d*) les nucléoles noyaux, ou noyaux en miniature, renfermant par conséquent tous les éléments d'un noyau véritable; membrane, portion plasmatique et portion nucléiniene.

In Lithobius, Scutigera, and Geophilus nucleoli of the fourth type, nucléoles noyaux were found by Carnoy. These are similar in general characteristics to the karyosphere in Scolopendra heros, although differing in many details. In Scolopendra dalmatica, however, according to Carnoy ('85), "L'élément nucléin d'ailleurs volumineux, est généralement irrégulier, bosseli, parfois moniliforme," and the nucleolus "n'est pas un nucléole-noyau mais un nucléole plasmatique." The structure of the nucleus "est donc celle d'un noyau ordinaire." The nucleolus does not stain with the chromatin stains and takes no part in the formation of the chromosomes, which arise directly from the chromatic network of the nucleus.

In attempting to correlate these results of Carnoy with my own observations upon American species of the same genus, one of two conclusions is necessary. Either Carnoy mistook the early prophase of the first spermatocyte for the "resting stage," or the condition of the chromatin in S. dalmatica presents yet another variation in its behavior from that

found in S. heros. In the light of these later observations upon S. subspinipes, the latter view seems probable.

If Carnoy's observations be accepted as correct, we have three variations in the behavior of the chromatin during the growth period; and these variations form a graded series. In Scolopendra dalmatica the chromatin, as in the majority of metazoa, is in the form of an apparent reticulum or spireme distributed irregularly throughout the nucleus; in S. subspinipes the chromatin threads are aggregated in a rather loose manner and are deposited upon the surface of the large nucleolus, and in S. heros the chromatin filaments are so densely massed in an approximately spherical body — containing no nucleolar material — that it is only in the most favorable cases that its true spireme structure can be observed.

Zoölogical Laboratory, Harvard University,
June 14, 1905.

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EXPLANATION OF PLATE.

All drawings are of *Scolopendra subspinipes* and were made by the author from camera lucida outlines at a magnification of 1800 diameters. They were reduced one third in reproduction, making a final magnification of 1200 diameters.

FIGURE 1. Prophase of the last spermatogonial division, showing the plasmosome with the accessory chromosome closely apposed to one side, and the other chromosomes lying free in the nucleus.

FIGURES 2, 3. Early and late telophase of the last spermatogonial division. In Figure 3 the accessory chromosome can be readily distinguished from the other chromosomes, which are granular filaments.

FIGURES 4, 5. Early spermatocytes. The nuclear membrane is reappearing and the chromatin segments of the reduced number are arranged irregularly throughout the nuclear area. Evidences of the origin of the elements by an end to end union of spermatogonial chromosomes is seen in the V-shaped character of most of them. In Figure 5 the plasmosome is arising in close relation with the accessory chromosome.

FIGURE 6. A pair of spermatocytes during the growth period. The plasmosome has increased in size and some of the chromosomes have become arranged upon its periphery. Others are still free in the nucleus.

FIGURE 7. Nucleus at a slightly later stage.

FIGURE 8. Series of figures (*a-f*) showing the evolution of the plasmosome and origin of the karyosphere.

FIGURES 9–12. Various appearances presented by the karyosphere during the "vesicle" stage.

FIGURE 13. Large spermatocyte in the vesicle stage.

FIGURE 14. Early prophase of a large spermatocyte. The chromatin has become detached from the plasmosme in the form of several granular masses.

FIGURES 15–18. Nuclei in the early prophase.

FIGURE 19. Mid prophase of a large spermatocyte, showing the character of the tetrads in Scolopendra subspinipes. The nucleolus is becoming more vacuolated.

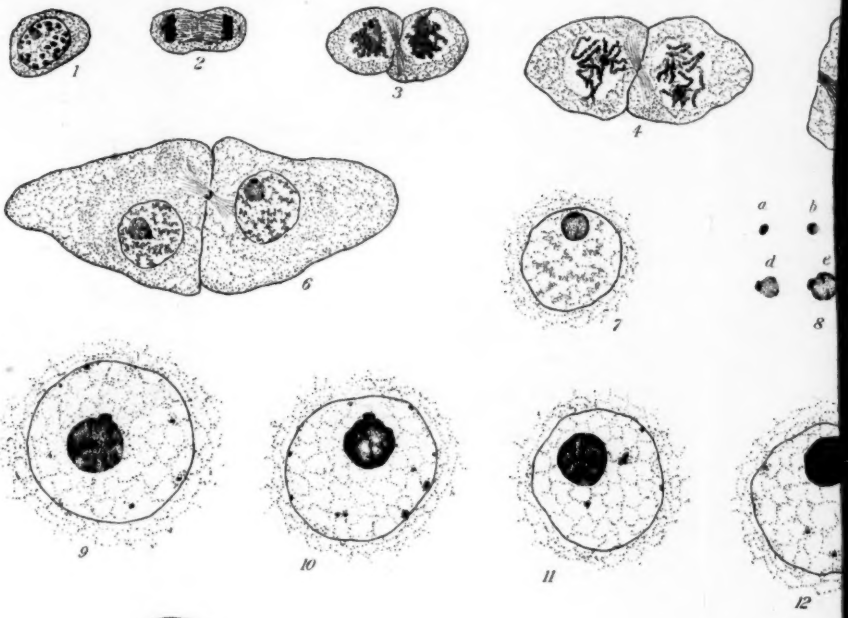
FIGURE 20. Later prophase. The tetrads have become condensed into homogeneous chromosomes, which are typically four-lobed.

FIGURE 21. Late prophase in a small spermatocyte.

FIGURE 22. Prophase of secondary spermatocyte.

FIGURE 23. Metaphase of a small second spermatocyte.

FIGURE 24. Spermatid of Scolopendra subspinipes.



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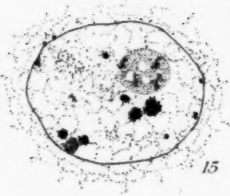

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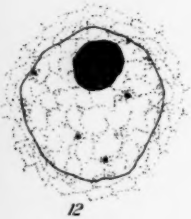

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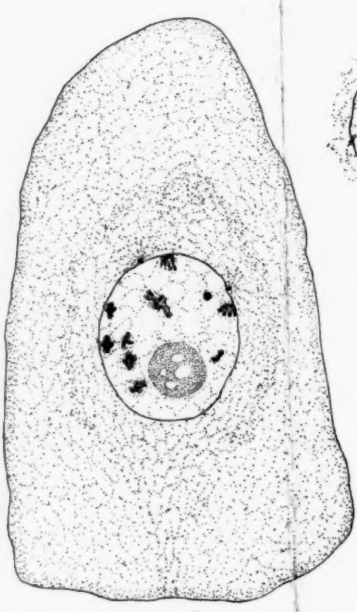

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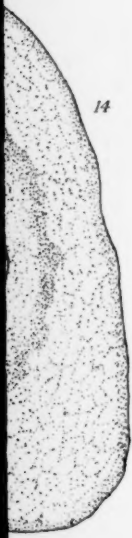

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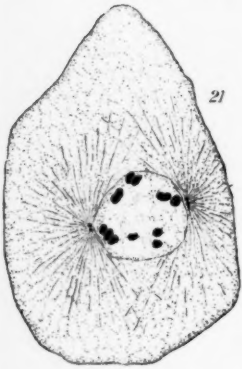

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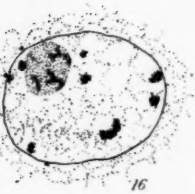
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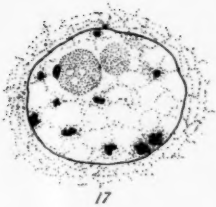
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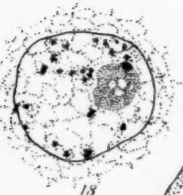
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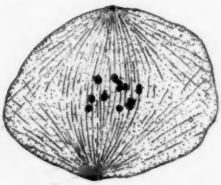
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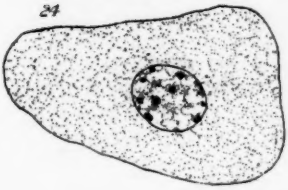
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